THE GEOTROPISM OF FRESHWATER SNAILS.[1]

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CONTENTS.

I. INTRODUCTORY.

Walter (10) and Dawson (2) have investigated the geotropic reactions of *Physa* and other freshwater snails in connection with their respiratory phenomena. However, their observations do not agree on certain points. Walter (10, p. 26) and Dawson (2, p. 93) agree with each other that freshwater snails are negatively geotropic, "when their lungs are empty." The snails being air-breathing forms, it is, of course, necessary for them to crawl up to the surface of water for their air supply, "although their specific gravity is meanwhile gradually increasing through exhaustion of the air," as Walter expresses it. For this upward crawling, the pull of gravity would be expected to act as a "directive force."

Walter and Dawson, however, depart from each other when they come to consider positive geotropism in these snails. The former states that, "after filling the lung with air, they are

[1] From the Physiological Laboratory of the University of Minnesota, Minneapolis.

positively geotropic," so that "they tend to climb down." The latter, on the other hand, states that when the snails "have sufficient air they become indifferent to gravity and crawl in all directions."

Moreover, they do not agree concerning the behavior of the snails from which "the air supply is cut off." According to Walter, "after reaching the highest point in the flask," which was in an inverted position in water, "and finding themselves unable to renew their supply, their ordinary behavior, to which there were some exceptions, was to let go and drop like dead weights" (10, p. 27). Dawson denies this statement of Walter as follows: "*Physa*, after they have been denied atmospheric air for some time, manifest indifference to the influence of gravity, and scatter over the sides and bottom of the bottle. They have never been observed to let go and drop like dead weights upon being denied atmospheric air" (2, pp. 104, 105).

In this paper an attempt has been made to compare certain experimental results obtained by the writer with those of his predecessors. A comparison is also made with other results obtained by the writer with marine snails.

The experimental work was done in the physiological laboratory of the University of Minnesota, under the direction of Professor E. P. Lyon, during the academic year of 1913–1914, while the writer was holding a Shevlin Fellowship. The writer expresses his appreciation of the interest and suggestions of Professor Lyon throughout the course of the work. To Professor John M. Holzinger, the principal of the State Normal School of Winona, Minn., the writer acknowledges indebtedness for the identification of the forms experimented upon.

II. Materials.

Common freshwater snails, *Physa gyrina* Say, *Planorbis trivolvis*, *Limnæa stagnalis*, and *Limnæa Columella*, were used for the work. The snails were kept in glass aquaria together with green algæ. They seemed to be perfectly healthy, and were observed to grow.

III. Experimental.

To study the behavior of an animal it is always necessary to discriminate the force under consideration as much as possible from other forces which may act simultaneously with it, favorably or antagonistically. Oxygen for pulmonate animals such as *Physa* is, of course, very important. That food is another factor in determining behavior of living animals need hardly be mentioned. Contact stimuli must also be considered. Light is often important. These with gravity are the chief forces which should be borne in mind.

The effect of the force of gravity on *Physa* and others is the problem with which this paper is chiefly concerned. But in considering this the other forces just mentioned must also be considered. Light especially must be taken into account.

1. Heliotropism of Physa gyrina Say.

Walter (10, pp. 23–24) has experimentally shown that *Physa primeana* Tyron and others are generally negatively heliotropic. A series of experiments was made with *Physa gyrina* Say to compare results with the results obtained by Walter. The experiments were conducted as follows: Five selected individuals were placed on a smooth glass plate with their anterior ends facing direct sunlight. The surface of the plate was carefully moistened. During experiments the angle of the rays of sunlight was about 22.5°. The glass plate was horizontally placed in air.

Table I.

Heliotropism of *Physa* on a Horizontal Moist Glass Plate in Air at the Angle of 22.5° of the Rays of Sunlight.

Table shows results after one minute. Feb. 14, 1914, 9:30 A. M. Temperature, 22° C.

No. of Animals.	No. of Trials.	— Heliotropism.		+ Heliotropism.		Horizontally Crawled.	
		No.	%.	No.	%.	No.	%.
1	20	20	100	0	0	0	0
2	20	20	100	0	0	0	0
3	20	20	100	0	0	0	0
4	20	10	50	4	20	6	30
5	20	4	20	16	80	0	0
Total 5	100	74	or 74%	20	or 20%	6	or 6%

The results, given in Table I. confirm Walter's conclusion. However, there are marked individual differences. Number 5, for instance, was exceptionally positive to light, while Numbers 1, 2, and 3 were always negative. Nevertheless, 74 per cent. were negative to light, and only 20 per cent. positive. From these results, the conclusion may be drawn that *Physa gyrina* Say is generally negatively heliotropic.

Dawson (2, pp. 60–61), on the other hand, has observed that darkness interferes with the activity of *Physa*. The writer's observations seem to be in accord with Dawson's. Five of the individuals above mentioned were kept in water under frequent observation one afternoon (from 2.40–4 P. M.) in darkness. Three of them were observed to crawl to the surface and then down again only two or three times; and two of them only once during the period, one 55 minutes and the other 70 minutes after being covered. The rest of the time they did not move at all.

2. *Geotropism of Physa and Other Species, with the Lung Empty and with the Lung Filled with Air.*

As already mentioned, Walter and Dawson disagree on their observations concerning positive geotropism in *Physa* and other species after the air supply is cut off. Neither has, however, furnished the quantitative evidence from which the conclusion was drawn. The writer, therefore, has made some quantitative observations on this point.

(*a*) *Observations on Physa.*—Five selected individuals of *Physa* were placed in a beaker containing about 300 c.c. of water. The beaker, which had vertical sides and a horizontal bottom, was placed as near as possible in optimum daylight. The water which was used for this purpose was taken from the dish in which *Physa* were kept, and was filtered when necessary. The following observations have two aspects, (1) response of *Physa* to gravity, when the lung is empty, and (2) when the lung is full of air. The results are given in Table II.

The negative geotropism of *Physa*, when its lung is empty, is precise and marked. It is impossible to mistake it. It is also evident, on the other hand, that the positive geotropism of the animal after filling the lung, though not as precise as the negative

geotropism observed when the lung is empty, is predominant in the majority of cases, that is, in over 90 per cent. Cases of "indifference" to gravity numbered less than 10 per cent. That *Physa* should become positive to gravity after taking in air supply seems to the writer to be quite natural, since the animal is primarily positively geotropic as will be shown later. Moreover, it is worth mention that each individual occasionally showed a peculiar "habit." It crawled up as usual, turned downward when it had reached the surface, and crawled down, making no effort to get air. The number of observations of this phenomenon for each individual is given for reference in Table II. in the second horizontal column and indicated by a star.

Table II.

Geotropism of *Physa* at the Angle of 90° of Inclination of a Support in Water, after Animals have taken Air in the "Lung-sac."

Dates.	Temp. of Water.	No. of Trials.	Animal No.	+ Geotropism.		"Indifferent to Gravity" (?)		
				Vertically or almost Vertically Oriented Downward and Crawled.	Diagonally Oriented Downward and Crawled.	Horizontally Oriented and Crawled.	Irregularly Crawled.	Crawled on the Surface-Film of Water.
Dec. 27, 3.10–4.05 P.M. Dec. 28, 3.25–3.50 P.M. Dec. 31, 10.35–11.15 A.M.	19° C.	18	1	7	3	2	1	1
			1*	3	1	0	0	0
		15	2	6	5	0	0	1
			2*	3	0	0	0	0
		11	3	5	1	0	1	0
			3*	4	0	0	0	0
		11	4	8	0	0	0	0
			4*	1	2	0	0	0
		19	5	13	0	0	0	1
			5*	5	0	0	0	0
		74	5	67 or 90.5%		7 or 9.4%		

(*b*) *Observations on Planorbis and Limnæa.*—With single individuals of these genera, the same tests as above were made and still more conclusive results were obtained. Since these snails were comparatively large forms, they were favorable for observation. If they were dislodged they fell to the bottom, provided their lungs were "relatively empty." If the lungs on the contrary were full of air, dislodged snails floated on the surface

of water. The same was true in the case of *Physa.* But with this species, as has been already pointed out, it was impossible to exclude light in the experiments because it was inactive in darkness. Consequently the negative heliotropism tended to blur the geotropism. This disadvantage was entirely removed in *Planorbis* and *Limnæa,* because these forms were active even in total darkness.

Observation 1: *Planorbis trivolvis* was put in the 600-c.c. beaker full of water. It either floated or sank, depending on the condition of its lung as above mentioned. If it floated, *i. e.*, was lighter than water, observation on positive geotropism was made; if it sank, *i. e.*, was heavier than water, observation on negative geotropism was made. Either event, therefore, was useful. At about two-minute intervals, the snail was dislodged by a test-tube cleaner, and then was covered by a dark-box. The results are given in Table III.

TABLE III.

Geotropism of *Planorbis trivolvis* on a Vertical Side of a Beaker Full of Water in Total Darkness When it Was Lighter than the Water. Table Shows Results Within Two Minutes.				Geotropism of *Planorbis trivolvis* on a Vertical Side of a Beaker Full of Water in Total Darkness When it Was Heavier than the Water. Table Shows Results After Two Minutes.			
Temp. of Water.	No. of Trials.	+ Geotropism.		Temp. of Water.	No. of Trials.	— Geotropism.	
		No.	%.			No.	%.
19° C.	30	30	100	19° C.	10	10	100

Discussion is hardly needed. A hundred per cent. in both positive and negative geotropisms was obtained. The orientation of positive geotropism in this snail was just as precise as that of negative geotropism.

Observation 2: In the same manner as above, *Limnæa stagnalis* was observed in total darkness. The results are given in Table IV.

TABLE IV.

Geotropism of *Limnæa stagnalis* on a Vertical Side of a Beaker of Water in Total Darkness When it Was Lighter than Water. Table Shows Results After Two Minutes.					Geotropism of *Limnæa stagnalis* on a Vertical Side of a Beaker of Water in Total Darkness When it Was Heavier than Water. Table Shows Results After Two Minutes.			
Temp. of Water.	No. of Trials.	+ Geotropism.		Did Not Move.	Temp. of Water.	No. of Trials.	— Geotropism.	
		No.	%.				No.	%.
19° C.	35	24	68.5	11 or 31.4%	19° C.	25	25	100

As may be seen from the table, the snail did not respond eleven times out of thirty-five trials, when it was lighter than water. This means that it was still floating when the complete two-minute interval was over. The failure of response to gravity in these cases need not be interpreted as "indifference" to gravity, because it was often observed that the snail had opened its air cavity at the time of observation. Evidently it was taking in more air. The geotropic response failed, therefore, because the lung was not full of air. All internal conditions being equal, the snail tends to crawl down, if its lung is full of air. If it crawled downward, it crawled vertically, orienting itself with its anterior end accurately in that direction.

Observation 3: *Limnæa columella*, again, when lighter than water, failed to respond to gravity nearly half the time, as Table V. has shown.

TABLE V.

Geotropism of *Limnæa columella* on a Vertical Side of a Beaker Full of Water in Total Darkness, When it was *Lighter* than the Water. Table Shows Results After Two Minutes.

Temp. of Water.	No. of Trials.	+ Geotropism.		Did Not Move.
		No.	%	
19° C	35	18	51.4	17 or 48.5%

Only a limited number of observations could be made at a sitting, as the animals ceased to respond at all. This was probably a fatigue effect.

It was observed three or four times that the snail crawled down with its shell in a horizontal position; and two or three times with the anterior end of its shell pointed up. It thus crawled down even against mechanical disadvantage.

The writer was unable to obtain satisfactory observations on this snail's negative geotropism. It crawled up to the surface for air. But when it was subjected to experimentation, it retreated into its shell and did not readily come out.

The writer by the above observations confirms Walter's conclusion regarding the effect of taking air on the geotropism of *Physa* and other species.

3. *Geotropism of Physa with Lung Empty and Filled with Air, in Presence of Food.*

Food being one of the strongest of forces in determining behavior, it was thought advisable to observe its effect on *Physa*. Green algæ were carefully placed on the bottom of the beaker in which there were five selected individuals of *Physa*. It was surprising to find that with food present *Physa* seldom crawled up to the surface for the air supply. After obtaining air moreover most of them crawled down just as precisely as they crawled up. It must also be added that they were not in a starving condition previous to these experiments.

It should be remembered, however, that in this case three forces, that is to say, (1) light, to which *Physa* is negative, (2) gravity, to which it is positive after taking in air, and (3) food, to which it is presumably positive, were here combined. The result of the combination of these three forces is the acceleration of positive geotropism. Negative geotropism, on the other hand, is retarded, even though it is very important for the air supply.

4. *Geotropism of Physa at the Different Angles of Inclination of the Supports in the Air and in Total Darkness.*

Imagining that negative and positive geotropisms of *Physa* and others are due only to respiratory phenomena, Walter claims that "so far as gravity alone is concerned, they should show no response at all" (10, p. 26). According to Dawson, geotropism (negative) is only possible "when their lungs are empty, but when they have sufficient air they become indifferent to gravity and crawl in all directions" (2, p. 93). In a certain sense, therefore, Walter and Dawson agree on this point. This contention will be experimentally examined in this section.

(*a*) *Experiments with a Plain Glass Plate.*—After a few trials it was found that *Physa* was *positively geotropic* even at a slight inclination of a plain glass plate in the air and in total darkness. The following method of experimentation was therefore adopted. The well-moistened glass plate being held slightly inclined, the animal was placed upon it with its head down. When five selected individuals had been so placed, the plate was reversed,

and was placed on a "rack" specially made for angle determination. The whole arrangement was covered as soon as possible with a dark box. Curiously enough, darkness seemed not to interfere very much with *Physa's* activity, if the experiment was conducted in the air, though it did interfere in water, as already shown. *Physa* oriented itself in the line of the force of gravity and crawled in that direction. The relative weight of *Physa* is about a thousand times as great in the air as in the water. This probably made a difference in its activity in the air even in total darkness.

The results given in Table VI. show that from the angle of 10¾° of inclination to that of 56¼°, positive geotropism increases as the degree of the angle increases. It should be added that this was not because the lung was full of air. On the contrary, about two thirds of these *positive* animals sank, when they were tested in water. This means that their lungs were empty. Negative geotropism and horizontal crawling, on the other hand, decrease in reverse proportion as the angle of inclination is increased. This was not because the lung was empty. On the contrary, about half of these *negative* animals floated, when they were tested in water.

But there was a limit to the degree of inclination of the support, beyond which *Physa* could not actively move on the plain glass plate on account of the force of gravity. This is significant. At the angle of 67½° positive geotropism suddenly decreases, and negative geotropism and horizontal crawling increase. Gravity, of course, is constant and always exerted vertically. But the effective force exerted on the animals depends upon the inclination of the surface on which the animals crawl. The exertion required to enable the animals to move on a horizontal surface is least; that required on a vertical surface is greatest. At the angle of 67½°, therefore, the effective force of gravity was so great that some individuals of *Physa* could not actively move against it (in air). An apparent increase of negative geotropism, therefore, was the result. This becomes clear, when one considers the failure of the experiments at the angle of 78¾°, which was due to the fact that nearly all the animals passively slid down the plate, mostly with their heads up. The optimum inclination

seems to be about 56°. The inference may be made that positive geotropism in *Physa* is an active process, and that negative geotropism, on the other hand,is due largely, though not entirely, to "passive orientation."

The so called mechanical theory of geotropism, however, can not be applied even in the case of negative geotropism. This is obvious when one remembers that *Physa* becomes negative to gravity when "its lung is empty," even though its specific gravity is less than that of water; and positive when its lung is full of air, even though its specific gravity is greater than that of water. The essential factors, therefore, which determine the geotropic orientation, either positive or negative, of *Physa* seem to be internal, that is, physiological ones (cf. 3, 4, 5, 7, 8 and 9 in the bibliography).

TABLE VI.

GEOTROPISM OF *Physa* AT THE DIFFERENT ANGLES OF INCLINATION OF A SMOOTH GLASS PLATE IN THE AIR IN TOTAL DARKNESS.

At beginning of experiments, each head placed upward. Table shows results after one minute.

Temp. of Room.	Angles.	No. of Trials.	No. of Animals.	+ Geotropism. Oriented and Crawled Downward.		− Geotropism. Crawled Upward.		Horizontally Crawled.	
				No.	%	No.	%	No.	%
20.5° C	67.5°	5	50	29	58	11	22	10	20
20.5° C	56¼°	5	50	47	94	1	2	2	4
20.5° C	45°	5	50	41	82	6	12	3	6
20.5° C	33¾°	5	50	35	70	11	22	4	8
20.5° C	22½°	5	50	31	62	12	24	7	14
20.5° C	11¼°	5	50	30	60	11	22	9	18
Total		30	300	213 or 71%		52 or 19.3%		35 or 11.6%	

From the above results the writer thinks that both Walter and Dawson overlooked the fact that *Physa* is naturally positively geotropic.

(*b*) *Experiments with a Ground-Glass Plate.*—Contact stimuli, as stated, affect the behavior of animals. Supposedly it might affect the geotropism of *Physa*. The same methods were used here as in the above. The results given in Table VII. show a fair agreement with the above supposition.

Table VII.

Geotropism of *Physa* at the Different Angles of Inclination of a Ground Glass Plate in Air in Total Darkness.

At beginning of experiment each head placed upward. Table shows results after one minute.

Temp. of Room.	Angles.	No. of Trials.	No. of Animals.	+ Geotropism. Oriented and Crawled Down.		— Geotropism. Crawled Up Not Quite Vertical.		Horizontally Crawled.		Not Moved.	
				No.	%.	No.	%.	No.	%.	No.	%.
20° C.	90°	10	50	38	76	0	0	5	10	7	14
	78¾°	10	50	41	82	1	2	5	10	3	6
	67½°	10	50	41	82	3	6	1	2	5	10
	56¼°	10	50	37	74	5	10	2	4	6	12
	45°	5	50	35	70	2	4	5	10	8	16
	33¼°	5	50	32	64	3	6	8	16	7	14
	22½°	5	50	28	56	5	10	4	8	13	26
	11¼°	5	50	24	48	11	22	11	22	4	8
Total.....		60	400	276 or 69%		30 or 7.5%		41 or 10%		53 or 13.5%	

Physa evidently could stick on the ground-glass plate better than on the plain glass plate, as would be expected. Experiments, therefore, could be carried on even at an angle of 90°. Here again, it is noticeable that there is a decrease of positive geotropism at this angle. The optimum inclination in this case is between the angles of 67½° and 78¾°.

5. *Summation of Gravity and Light Stimuli.*

Physa being positive to gravity and negative to light, as already seen, it would be expected to crawl downward even at a small angle of inclination, if it were placed in a strong light. This is just what happened. One morning the rays of sunlight were falling at an angle of about 11¾°. The angle of the rays of sunlight was nearly constant during the experiments. Ten selected individuals were carefully placed with their heads down on a moist plain glass plate. The plate was then reversed and put on the rack whose angle of inclination was 11¾°. They all oriented themselves away from the rays of sunlight, that is, downward, and crawled in that direction. Ten trials were made and there was no exception.

Besides the above, observations on exclusion of the air were attempted, but the results were not satisfactory. Generally speaking however, Dawson's observations seem to be right, although the writer observed one individual "drop" once.

IV. Summary and Conclusion.

1. *Physa gyrina* Say is negatively heliotropic. It becomes sluggish in its activity in darkness, particularly in water.

2. *Physa gyrina* Say, *Planorbis trivolvis*, *Limnæa stagnalis*, and *Limnæa columella*, are negatively geotropic when their lungs are empty; and positively geotropic when their lungs are full of air. *Physa* often comes near the surface and crawls down again without filling its lung with air.

3. *Physa*, when put with green algæ, does not often crawl to the top.

4. At different angles of inclination of a plain glass plate in the air and in total darkness, *Physa* is positively geotropic. There is a certain limit of inclination beyond which the animal can not actively move on account of the force of gravity.

(*a*) Many of the individuals in question are positive to gravity, even though their lungs are empty.

(*b*) The optimum inclination of the plain glass plate on which *Physa* may crawl is an angle of 56¼°.

(*c*) At the angle of 67½°, positive geotropism decreases as negative geotropism and horizontal crawling increase. The negative geotropism is not necessarily the result of lack of oxygen.

(*d*) At the angle of 78¾° no experiments are successful.

5. At different angles of inclination of a ground-glass plate in the air and in total darkness, *Physa* reacts to gravity in a similar manner as though on the plain glass plate, although the limit of inclination is a little higher in the former than in the latter. The optimum inclination of the ground-glass plate is between the angles of 67½° and 78¾°.

6. Contact stimuli seem to interfere slightly with the geotropism of *Physa*.

7. The combination of gravity and light (both the glass support and the rays of light being inclined 11¾° to the horizontal) accelerates positive geotropism of *Physa*.

From the data here given the writer is inclined to draw the conclusion that *Physa* is naturally positively geotropic. It is little wonder, therefore, that *Physa* becomes positive to gravity when its lung is filled with air.

As to the organ of geotropic orientation of *Physa* and other snails, no direct experimental evidence is yet furnished. But

according to Cooke (1, p. 196), *Limnæa*, *Planorbis* and *Physa* have statocysts, which are situated near the pedal ganglion, and are probably connected with the cerebral. The statocyst also contains statoliths. The number of the statoliths "varies in different genera and species." There are a hundred in *Limnæa stagnalis* on which the writer has experimented, but about fifty in *Planorbis contratus* and *Physa fontinalis*. Therefore, *Planorbis trivolvis* and *Physa gyrina* Say very probably have statoliths. These statocysts with statoliths may be the organs for geotropic orientation. At any rate, the most probable factors of geotropic orientation, positive or negative, seem to be internal, that is, physiological, and not external.

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